Biol Fertil Soils (1999) 29:92–97

ORIGINAL PAPER

Peter D. Stahl · Timothy B. Parkin
Martha Christensen

Fungal presence in paired cultivated and uncultivated soils in central Iowa, USA

Received: 12 October 1997

Abstract Amounts of fungal biomass in adjacent cultivated and uncultivated soils in central Iowa were estimated and compared by quantifying soil ergosterol concentrations and lengths of fungal hyphae present. Both indices of fungal biomass, with one exception, indicated that there was at least twice as much fungal biomass in uncultivated soil as in cultivated soil. Levels of microbial biomass carbon in uncultivated soils were also determined to be at least twice that in cultivated soils. Data collected in this study indicate that fungi may be more significantly affected by agricultural soil management practices than other components of the soil microbial community. For two of the soils examined, calculated estimates denote that fungal biomass carbon represented approximately 20% of the total microbial biomass carbon in cultivated soil and about 33% of the microbial biomass carbon in uncultivated soil. Results of this study indicate that conventional agricultural practices result in a significant reduction of fungal biomass production in soil. Implications of differences in fungal biomass between the soils are discussed.

Key words Fungi · Soil ecology · Sustainable agriculture · Tillage · Prairie

P. D. Stahl
Department of Renewable Resources, University of Wyoming, Laramie, WY 82071, USA

T. B. Parkin
USDA – ARS, National Soil Tilth Laboratory, Ames, IA 50011, USA

M. Christensen
Department of Botany, University of Wyoming, Laramie, WY 82071, USA

Introduction

Fungi often represent the largest component of microbial biomass in arable soils (Gray and Williams 1971; Anderson and Domsch 1975) and make critical contributions to soil properties and processes (Harley 1971; Christensen 1989). As a group, fungi are primarily responsible for the decomposition and mineralization of organic residues in soil (Paul and Clark 1989), represent large nutrient pools (Whittaker 1975), make up an important food source for other soil organisms (Hunt et al. 1987; de Ruiter et al. 1994) and contribute to soil aggregate formation (Tisdall and Oades 1982). These activities make fungi critically important to soil quality and the sustainability of agroecosystems (Eash et al. 1994; Doran and Linn 1994).

A tremendous range in values exists in the amount of fungi reported to occur in different soils. For example, Baath and Soderstrom (1979) estimated the length of fungal hyphae in the A horizon of a Swedish coniferous forest soil to be 66900 m g^{-1} dry soil and calculated an estimate of fungal biomass in that horizon of 35.1 mg g^{-1} dry soil. In contrast, Stahl and Parkin (1996) reported estimates of 146 m g^{-1} dry soil and 0.06 mg g^{-1} dry soil for the length of fungal hyphae and total fungal biomass, respectively, in an agricultural soil in Iowa. Soils with such disparate fungal contents may be expected to differ in a number important ways, including potential rates of decomposition and mineralization, the amounts, forms and pools of nutrients as well as in water holding capacity and resistance to erosion.

Agricultural systems may be considered to be disturbed ecosystems as a result of tillage practices, water and nutrient inputs and pesticide applications (Zak 1992). Physical disturbance of the soil caused by tillage and residue management is a crucial factor in determining biotic activity and species diversity in agroecosystems (Doran and Werner 1990; Heisler and Kaiser 1995). Numerous studies have reported negative im-

pacts of agricultural practices such as tillage and pesticide application on levels of microbial biomass in soil (Lynch and Panting 1980; Schnurer et al. 1985; Doran 1987; Gupta and Germida 1988). For example, 16 years of tillage to soils in western Nebraska resulted in significant reductions in microbial respiration and total microbial biomass (48–64%) as compared to native sod (Follett and Schimel 1989). Specific effects of agricultural practices on soil fungi are less known but, according to Gochenaur (1981), species composition changes and species richness decreases following cultivation and management for monoculture crop production. In a study comparing the effects of different tillage practices on soil microbial biomass, Doran (1980) found that levels of fungal biomass were significantly greater under no-till soil management than under conventional tillage. Bloem et al. (1994) determined that fungal biomass in soil was 1.54 times greater in a winter wheat field under integrated management than under conventional management. Beare et al. (1993) reported that fungal community structure and hyphal density in soil were both strongly affected by tillage.

The objectives of the current study are to (1) compare amounts of fungal biomass in adjacent cultivated and uncultivated soils and (2) discuss the implications of the differences in fungal presence at the compared sites.

Materials and methods

Soil samples were collected from three sites in central Iowa (Table 1) during the first 2 weeks of June 1994. Sites were selected where virgin or established (>80 years old) prairie remnants lay immediately adjacent to and within the same soil map unit as cultivated cropland. Conventional tillage practices utilized at the cultivated sites examined include fall chisel plowing to a depth of ca. 20 cm and spring surface disking before seeding. Annual precipitation in the area sampled averages 84 cm (50-year average), with 72 cm as rain.

Eight soil cores (2.5 cm diameter) were taken randomly from within a 10 m circular area at each subsite. That portion of the core representing soil depth from 5 to 15 cm was placed in a small plastic bag and refrigerated (4 °C) immediately upon return to the laboratory. In preparation for analysis, each core was broken up and thoroughly homogenized. Five grams of each sample were added to 15 ml cold (2 °C) methanol and stored at 2 °C for analysis of ergosterol content. One gram of each sample was used for examination of total hyphal length and a 5 g subsample was used for gravimetric determination of soil moisture content. All subsamples were prepared within 24 h of sample collection.

Direct microscopic examination of fungal hyphae in soil was conducted using the membrane filter method (Hanssen et al. 1974) with calcofluor M2R white for observation of total fungal hyphal length. Calcofluor-stained slides were prepared as described by Stahl et al. (1995) except that prepared filters were immediately mounted on slides with one drop of immersion oil (as opposed to being allowed to dry for a few seconds). All slides were prepared within 24 h of sample collection. For each site, eight slides were made (one slide per soil core or sample) as was indicated as an efficient method by the results of our previous study (Stahl et al. 1995).

Slides were examined with a Nikon Microphot-SA epifluorescent microscope equipped with a high-intensity mercury light source and a Nikon UV-1A-filter cube. Observations were made using a dry 40× objective, 10× eyepieces, and a 1.5× light path magnifier (total magnification– 600×). Twenty five randomly chosen fields of view were counted on each slide.

Ergosterol was extracted from soil subsamples and quantified as described by Eash et al. (1996) and Stahl and Parkin (1996). Microbial biomass carbon in soil samples was determined by chloroform fumigation and extraction with 0.5 M K_2SO_4 on 25 g sieved field moist soil samples (Tate et al. 1988; Horwath and Paul 1994). Organic carbon in the fumigated and non-fumigated extracts was measured using a Dohrman Total Carbon Analyzer (Rosemont Analytical Services, Santa Clara, Calif.). Biomass carbon was calculated using a correction factor of 0.33 (Sparling and West 1988).

Wet aggregate stability was assessed according to methods described by Eash et al. (1994). Briefly, 200 g field moist soil was placed on a nest of sieves (8, 4, 2, 1, 0.5, 0.053 mm) and immersed in water. Samples were agitated using a sieving machine similar to the machine illustrated in Low (1954) for 5 min at 130 strokes min^{-1} (stroke length = 1.8 cm). Samples from the sieve were combined, oven dried (105 °C) and sand removed according to the procedure of Cambardella and Elliot (1992). Aggregation is reported as the percentage of soil (minus sand) present as aggregates greater than 0.505 mm.

Estimates of components of fungal biomass (total, living and non-living fungal biomass) in soils were based upon measurements of total fungal hyphal length and soil ergosterol concentration. First, living fungal biomass estimates were calculated using the method of Stahl and Parkin (1996). Non-living fungal biomass, which is basically the weight of empty hyphae or just the cell wall, was estimated by first determining what portion of the

Table 1 Sites sampled

Site	Soil	Location/description
1. Mcfarland, Park uncultivated	Lester sandy loam (Mollic Hapludalf)	Storey County, IA Restored upland tallgrass prairie site, restoration initiated in 1980.
2. Mcfarland, Park cultivated	Lester sandy loam (Mollic Hapludalf)	Storey County, IA In corn/soybean rotation
3. Doolittle Prairie, cultivated	Kossuth silty clay loam (Typic Haplaquoll)	Storey County, IA, T85N, R23W, NW1/4 Sec 25 Cultivated for over 100 years, past 10 years in corn/soybean rotation
4. Doolittle Prairie, uncultivated	Kossuth silty clay loam (Typic Haplaquoll)	Never tilled native prairie; mesic site vegetated by mixed grasses and forbes
5. Railroad Site, cultivated	Webster clay loam (Typic Hapludoll)	Storey County, IA, T85N, R22W, NW1/4 Sec 20 In corn/soybean rotation
6. Railroad Site, uncultivated	Webster clay loam (Typic Hapludoll)	Restored tallgrass prairie ca. 80 years old

total hyphal length was living fungal biomass using the equation given by Paul and Clark (1989):

$$B_f = \pi r^2 L e S_c$$

where B_f is fungal biomass, r is hyphal radius (using an average value of 1.5 μm based on observation and measurement of hyphae from the soil samples), L is hyphal length (cm g^{-1} soil), e is hyphal density (1.3 g cm^{-3}), and S_c is solids content (0.3). Living hyphal length was estimated by entering our calculated value for living fungal biomass and solving for length. An estimate of non-living hyphal length was obtained by subtracting living hyphal length from the total hyphal length determined by direct microscopic counting. Biomass of non-living hyphae can be estimated by first calculating its surface area using the equation:

$$SA_n = 2\pi r L_n$$

where SA_n is surface area of non-living hyphae, r is hyphal radius (using an average value of 1.5 μm based on observation and measurement of hyphae from the soil samples) and L_n is the length of non-living hyphae. The value for non-living hyphal surface area was then multiplied by the cell wall thickness (using an average value of 0.1 μm) to give an estimate of the biomass of non-living hyphae (density of chitin was assumed to be 1.0). Values for the biomass of living and non-living hyphae were summed to estimate total fungal biomass.

Calculations of amount of nutrients in fungal biomass in the Doolittle soils were made using median values for carbon and nitrogen content of fungal tissue of 45% and 7%, respectively.

Results

Mean values for total hyphal length (living and non-living) and soil ergosterol content for each of the three sites examined are given in Fig. 1. Hyphal length values ranged from a high of 1269 m g^{-1} dry soil in uncultivated soil at the Doolittle site to a low of 157 m g^{-1} dry soil in cultivated soil at the Mcfarland site. Soil ergosterol content was greatest in uncultivated soil at the Railroad site (3.67 μg g^{-1} soil) and lowest in cultivated soil at the Mcfarland site (1.02 μg g^{-1} soil). It is interesting that the ranking of the soils based on total hyphal lengths was slightly different from the ranking based on ergosterol content. That is, the cultivated soil at the Doolittle site had a lower ergosterol content but greater amount of fungal hyphae than did the cultivated soil at the Railroad site. Both measures of fungal

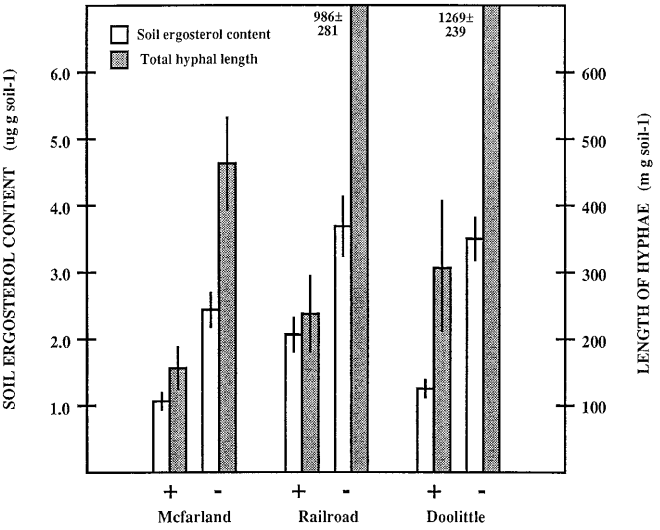

Fig. 1 Soil ergosterol content and total hyphal length (living and nonliving) in each of the soils examined (+, cultivated; −, uncultivated). *Vertical bars* represent ±1 SD deviation

biomass, with the exception of ergosterol at the Railroad site, indicate that there was at least twice as much fungal tissue in uncultivated soil than in cultivated soil.

Calculated estimates of living, non-living and total fungal biomass based on amounts of ergosterol and total hyphal length at the three sites examined are given in Table 2. Living biomass estimates ranged from 0.06 mg g^{-1} soil to 0.66 mg g^{-1} soil and were always greater for uncultivated soil than for cultivated soil. Ratios of living biomass in uncultivated soil to cultivated soil varied from 3.8:1 at the Mcfarland and Railroad sites to 6.6:1 at the Doolittle site, where the original prairie soil has never been tilled. Non-living biomass estimates varied from 0.13 mg g^{-1} soil to 0.97 mg g^{-1} soil and, as in the case of living biomass estimates, were always greater in uncultivated soil. Differences in the estimated amounts of non-living biomass in the paired soils were not as great as in living biomass estimates. Ratios

Table 2 Estimates of microbial biomass and components of fungal biomass in soil at the three sites examined

Site	Estimated living fungal biomass		Estimated non-living fungal biomass		Estimated total fungal biomass		Estimated total microbiall biomass	
	(mg g^{-1} soil)	(kg ha^{-1})	(mg g^{-1} soil)	(kg ha^{-1})	(mg g^{-1} soil)	(kg ha^{-1})	(mg C g^{-1} soil)	(kg C ha^{-1})
Mcfarland Park								
Cultivated	0.06	340	0.13	730	0.19	1070	0.48 ± 0.05[a]	2690 ± 280
Uncultivated	0.23	1080	0.35	1640	0.58	2720	1.05 ± 0.20	4950 ± 943
Doolittle Prairie								
Cultivated	0.10	350	0.25	880	0.35	1230	0.79 ± 0.10	2770 ± 351
Uncultivated	0.66	1620	0.97	2460	1.63	4100	2.20 ± 0.44	5410 ± 1082
Railroad Site								
Cultivated	0.15	500	0.17	640	0.32	1140	0.76 ± 0.12	2550 ± 403
Uncultivated	0.57	1470	0.73	2090	1.30	3560	1.95 ± 0.51	5030 ± 1315

[a] Values given for estimated total microbial biomass are mean ± standard deviation

Table 3 Ratios of total fungal biomass in uncultivated to cultivated soil and total microbial biomass carbon to total fungal biomass carbon at the three sites

Site	Fungal biomass ratio uncultivated:cultivated	Ratio of total microbial biomass carbon to fungal biomass carbon
Mcfarland Park	3.2:1	
Cultivated		5.6:1
Uncultivated		4.0:1
Doolittle Prairie	4.7:1	
Cultivated		5.0:1
Uncultivated		2.9:1
Railroad Site	4.1:1	
Cultivated		4.9:1
Uncultivated		3.1:1

Table 4 Soil characteristics at the three sites

Site	pH	Bulk density (g cm^3)	Macroaggregates (%)	Organic C (%)	Organic N (%)
Mcfarland Park					
Cultivated	5.42	1.87	53.2 ± 3.88[a]	1.45 ± 0.14	0.13 ± 0.01
Uncultivated	6.05	1.57	68.4 ± 3.48	2.23 ± 0.39	0.17 ± 0.03
Doolittle Prairie					
Cultivated	6.78	1.17	54.0 ± 7.31	3.12 ± 0.29	0.24 ± 0.03
Uncultivated	5.58	0.82	67.4 ± 5.79	6.66 ± 0.81	0.47 ± 0.04
Railroad Site					
Cultivated	6.03	1.12	48.3 ± 6.22	3.38 ± 0.50	0.27 ± 0.04
Uncultivated	6.09	0.86	71.3 ± 2.08	6.78 ± 0.72	0.48 ± 0.07

[a] Values given for macroaggregates, organic C and organic N are mean standard deviation

of non-living biomass in uncultivated to cultivated soil ranged from 2.8:1 at the Mcfarland site to 4.3:1 at the Railroad site. Calculated estimates of total fungal biomass for the three sites indicate there was three to nearly five times more fungal biomass in uncultivated soil than in cultivated soil (Table 3).

The amount of microbial biomass carbon (Table 2) in uncultivated soils was also found to be at least twice that in cultivated soils. Uncultivated soil from the Doolittle prairie site, which had highest levels of total fungal biomass also had the greatest amount of microbial biomass carbon. With the exception of the cultivated soil from the Mcfarland site, ranking of sites based on microbial biomass carbon was identical to ranking based on estimated total fungal biomass.

Analyses of soil properties at the three sites revealed that uncultivated soils always had lower bulk densities and higher content of macroaggregates, organic carbon and organic nitrogen than cultivated soils (Table 4). At all three sites, fungal biomass as a proportion of microbial biomass was greater in uncultivated soils than in cultivated soils.

Discussion

Measurements of total fungal hyphal length and soil ergosterol concentrations as well as calculated estimates of living, non-living and total fungal biomass all indicate that the uncultivated soils examined in this study contain much larger quantities of fungal biomass than do the cultivated soils.

A number of practices associated with crop production can, directly or indirectly, negatively affect microbial biomass levels in soil. Agricultural management influences the activity of soil microorganisms predominantly through changes in soil environmental conditions (Doran and Werner 1990). Management practices can affect such factors as soil temperature and availability of water and oxygen. Various methods of tillage cause different degrees of soil disturbance and regular disturbances by tillage prevent long-term successional development of soil ecosystems (Doran and Werner 1990). Tillage disrupts hyphal networks in the soil and prevents accumulation of plant residues on the soil surface which buffer soil temperature and moisture conditions. Removal of large amounts of crop biomass for uses such as grain, hay or silage reduces the amount of available substrate to saprotrophic fungi. Lower levels of belowground root production, compared to that in the original native plant community, and phosphorus fertilization also adversely affect mycorrhizal fungi which can account for a significant portion of the total fungal biomass in a soil.

The implications of low levels of fungal biomass in soil as a result of disturbance are many and may lead to

a reduction in soil productivity and adversely affect the sustainability of agroecosystems. As the group of soil microorganisms primarily responsible for the decomposition of organic residues (Paul and Clark 1989), fungi are critically involved in nutrient cycling and soil fertility as well as the formation of soil organic matter and development and maintenance of soil structure.

Fungal biomass may represent a large pool of nutrients in many soils, especially in grassland soils where the annual growth and turnover of fine roots supports an equally active and absorptive network of fungal hyphae. For example, uncultivated native prairie soil at the Doolittle site was estimated to contain ca. 1.66 mg fungal biomass g^{-1} dry soil which includes 0.66 mg living and 1.00 mg non-living fungal biomass. Extrapolating these values to a larger volume converts these figures to ca. 4100 kg fungal biomass ha^{-1} to a depth of 0.3 m (ca. 1 ft). Assuming that fungal biomass (both living and non-living) is composed of about 45% carbon and 7% nitrogen, fungal biomass in uncultivated soil at the Doolittle site contains ca. 1845 kg carbon and 287 kg nitrogen ha^{-1} to a depth of 0.3 m. In contrast, cultivated soil at the Doolittle site contains ca. 1230 kg fungal biomass ha^{-1} which represents pools of ca. 553 kg carbon and 86 kg nitrogen ha^{-1} to a depth of 0.3 m. These differences in the amount of nutrients held in organic form in the fungal biomass pool constitute important differences in total nutrient status of the cultivated and uncultivated soils. Data collected in our study show that at both the Doolittle and Railroad sites, uncultivated soils contain at least twice as much carbon in organic form and almost twice as much nitrogen in organic form as adjacent cultivated soils (Table 4).

Most of the carbon in the fungal biomass pool is immobilized in chitin, as the majority of fungal tissue in soil is non-living (Table 2), consisting of empty hyphal filaments. Because chitin is more slowly decomposed than biomass of other organisms, especially bacteria, carbon in fungal biomass may be more slowly lost from the soil system and represent a relatively stable form of soil organic matter (Holland and Coleman 1987). DeLuca and Keeney (1993) reported that the internal nitrogen cycle in soils of native and established prairies is highly conservative of nitrogen and that of cultivated soils has a much greater potential for nitrogen loss through denitrification and leaching. The efficiency of the nitrogen cycle in prairie soils has been partly attributed to the quality and quantity of available carbon substrate to enable microbial immobilization of large amounts of nitrogen relative to cultivated soils. Our finding of much larger amounts of fungal and total microbial biomass in prairie soils than in adjacent cultivated soils supports that hypothesis.

Fungi are known to play a major role in soil aggregation (Martin and Waksman 1940; Eash et al. 1994) and contribute to aggregate stability through both mechanical binding by fungal hyphae and chemical binding by fungal-produced polysaccharides (Lynch and Bragg 1985; Tisdall 1991). Our data show higher macroaggregate content in uncultivated soil than in cultivated soil at all three sites (Table 4). An increase in soil erodibility may be a serious consequence of conventional agricultural practices which reduce levels of fungal biomass.

Data collected in this study indicate that fungi may be more significantly affected by agricultural soil management practices than other components of the total soil microbial biomass pool. Assuming that fungal biomass is 45% carbon (Paul and Clark 1989), estimates of the amount of carbon in the total fungal biomass pool can be calculated for each soil. For the Doolittle Prairie soils, fungal biomass carbon represents approximately 20% of the total microbial biomass carbon in cultivated soil and about 34% of the microbial biomass carbon in uncultivated soil. Values for the Railroad site soils are very similar with fungal biomass carbon making up 20% of the microbial biomass carbon in cultivated soil and 32% in uncultivated soil.

In summary, examination of the length of fungal hyphae (living and non-living) and ergosterol content of paired cultivated and uncultivated soils in central Iowa indicates that conventional agricultural practices result in a reduction in the amount of fungal biomass produced in cultivated soil. The decrease in fungal biomass may be a result of altered soil environmental conditions resulting from tillage, lower annual litter input of agroecosystems compared to native plant communities, and direct disturbance of fungal mycelial networks by tillage.

References

Anderson JPE, Domsch KH (1975) Measurements of bacterial and fungal contributions to respiration of selected agricultural and forest soils. Can J Microbiol 21:314–322

Baath E, Soderstrom B (1979) Fungal biomass and fungal immobilization of plant nutrients in Swedish coniferous forest soils. Rev Ecol Biol Sol 16:477–489

Beare MH, Pohlad BR, Wright DH, Coleman DC (1993) Residue placement and fungicide effects on fungal communities in conventional and no-tillage soils. Soil Sci Soc Am J 57:392–399

Bloem J, Lebbink G, Zwart KB, Bouwman LA, Burgers SLGE, Vos JA de, Ruiter PC de (1994) Dynamics of microorganisms, microvores and nitrogen mineralisation in winter wheat fields under conventional and integrated management. Agric Ecosyst Environ 51:129–143

Cambardella CA, Elliot ET (1992) Particulate soil organic matter changes across a grassland cultivation sequence. Soil Sci Soc Am J 56:777–783

Christensen M (1989) A view of fungal ecology. Mycologia 81:1–19

DeLuca TH, Keeney DR (1993) Soluble organics and extractable nitrogen in paired prairie and cultivated soils of central Iowa. Soil Sci 155:219–228

Doran JW (1980) Microbial changes associated with residue management with reduced tillage. Soil Sci Soc Am J 44:518–524

Doran JW (1987) Microbial biomass and mineralizable nitrogen distributions in no-tillage and plowed soils. Biol Fertil Soils 5:68–75

Doran JW, Linn DM (1994) Microbial ecology of conservation management systems. In: Hatfield JL, Stewart BA (eds) Soil biology effects on soil quality. CRC Press, Boca Raton pp 1–27

Doran JW, Werner MR (1990) Management and soil biology. In: Francis CA, Flora CB, King LD (eds) Sustainable agriculture in the temperate zone. Wiley, New York, pp 205–230

Eash NS, Karlen DL, Parkin TB (1994) Fungal contributions to soil aggregation and soil quality. In: Doran JW, Coleman DC (eds) Defining soil quality for a sustainable environment. Soil Science Society of America Special Publication 35. Soil Sci Soc Amer, Madison, Wis., pp 221–228

Eash NS, Stahl PD, Parkin TB, Karlen DL (1995) A simplified method for extraction of ergosterol from soil. Soil Sci Soc Am J 60:468–471

Follett RF, Schimel DS (1989) Effect of tillage practices on microbial biomass dynamics. Soil Sci Soc Am J 53:1091–1096

Gochenauer SE (1981) Response of soil fungal communities to disturbance. In: Wicklow DT, Carroll GC (eds) The fungal community: its organization and role in the ecosystem. Marcel Dekker, New York, pp 459–479

Gray TRG, Williams ST (1971) Microbial productivity in soil. In: Hughes DE, Rose AH (eds) Microbes and biological productivity. Cambridge University Press, Cambridge, pp 255–286

Gupta VVSR, Germida JJ (1988) Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation. Soil Biol Biochem 20:777–786

Hanssen JF, Thingstad TF, Goksoyr J (1974) Evaluation of hyphal lengths and fungal biomass in soil by a membrane filter technique. Oikos 25:102–107

Harley JL (1971) Fungi in ecosystems. J Ecol 59:653–668

Heisler C, Kaiser E-A (1995) Influence of agricultural traffic and crop management on collembola and microbial biomass in arable soil. Biol Fertil Soils 19:159–165

Holland EA, Coleman DC (1987) Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68:425–433

Horwath WR, Paul EA (1994) Microbial biomass. In: Weaver RW, Angle S, Bottomley P, Bexdicek D, Smith S, Tabatabai A, Wollum A (eds) Methods of soil analysis, part 2. Microbiological and biochemical properties. Soil Science Society of America, Madison, Wis., pp 753–773

Hunt HW, Coleman DC, Ingham ER, Ingham RE, Elliot ET, Moore JC, Rose SL, Reid CPP, Morley CR (1987) The detrital food web in a shortgrass prairie. Biol Fertil Soils 3:57–68

Low AJ (1954) The study of soil structure in the field and in the laboratory. J Soil Sci 5:57–78

Lynch JM, Bragg E (1985) Microorganisms and soil aggregate stability. Adv Soil Sci 2:133–171

Lynch JM, Panting LM (1980) Cultivation and the soil biomass. Soil Biol Biochem 12:29–33

Martin JP, Waksman SA (1940) Influence of microorganisms on soil aggregation and erosion. Soil Sci 50:29–47

Paul EA, Clark FE (1989) Soil microbiology and biochemistry. Academic Press, San Diego

Ruiter PC de, Bloem J, Bouwman LA, Didden WAM, Hoenderboom GHJ, Lebbink G, Marinissen JCY, Vos JA de, Vreeken-Buijs MJ, Zwart KB, Brussard L (1994) Simulation of dynamics in nitrogen mineralisation in the belowground food webs of two arable farming systems. Agric Ecosyst Environ 51:199–208

Schnurer JM, Clarholm M, Rosswall T (1985) Microbial biomass and activity in an agricultural soil with different organic matter contents. Soil Biol Biochem 17:611–618

Sparling GP, West AW (1988) A direct extraction method to estimate soil microbial biomass C: calibration in situ using microbial respiration and 14C labelled cells. Soil Biol Biochem 20:337–343

Stahl PD, Parkin TB (1996) Relationship of soil ergosterol concentration and fungal biomass. Soil Biol Biochem 28:847–855

Stahl PD, Parkin TB, Eash NS (1995) Sources of error in direct microscopic methods for estimation of fungal biomass in soil. Soil Biol Biochem 27:1091–1097

Tate KR, Ross DJ, Felthan CW (1988) A direct extraction method to estimate soil microbial biomass C: effects of some experimental variables and some different calibration procedures. Soil Biol Biochem 20:329–355

Tisdall JM (1991) Fungal hyphae and structural stability of soil. Aust J Soil Res 29:729–743

Tisdall JM, Oades JM (1982) Organic matter and water-stable aggregates in soils. Soil Sci 33:141–163

Whittaker RH (1975) Communities and ecosystems. Macmillan, New York

Zak JC (1992) Response of soil fungal communities to disturbance. In: Wicklow DT, Carroll GC (eds) The fungal community: its organization and role in the ecosystem. Dekker, New York, pp 403–425